Post-Establishment Movement of Western Corn Rootworm Larvae (Coleoptera: Chrysomelidae) in Central Missouri Corn

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ABSTRACT If registered, transgenic corn, *Zea mays* L., with corn rootworm resistance will offer a viable alternative to insecticides for managing *Diabrotica* spp. corn rootworms. Resistance management to maintain susceptibility is in the interest of growers, the Environmental Protection Agency, and industry, but little is known about many aspects of corn rootworm biology required for an effective resistance management program. The extent of larval movement by the western corn rootworm, *Diabrotica virgifera virgifera* LeConte, that occurs from plant-to-plant or row-to-row after initial establishment was evaluated in 1998 and 1999 in a Central Missouri cornfield. Post-establishment movement by western corn rootworm larvae was clearly documented in two of four treatment combinations in 1999 where larvae moved up to three plants down the row and across a 0.46-m row. Larvae did not significantly cross a 0.91-m row after initial host establishment in 1998 or 1999, whether or not the soil had been compacted by a tractor and planter. In the current experiment, western corn rootworm larvae moved from highly damaged, infested plants to nearby plants with little to no previous root damage. Our data do not provide significant insight into how larvae might disperse after initial establishment when all plants in an area are heavily damaged or when only moderate damage occurs on an infested plant. A similar situation might also occur if a seed mixture of transgenic and isoline plants were used and if transgenic plants with rootworm resistance are not repellent to corn rootworm larvae.

KEY WORDS western corn rootworm, *Diabrotica virgifera virgifera*, larval movement, resistance management

SINCE THE EMERGENCE of the western corn rootworm, *Diabrotica virgifera virgifera* LeConte, as a major pest of corn, *Zea mays* L., >50 yr ago, a variety of management tactics have been implemented, but many have failed. Because their eggs overwinter in the soil and hatch the following spring, rotating corn to a nonhost, such as soybeans, *Glycine max* L., has generally been an effective management strategy. However, both the western corn rootworm and northern corn rootworm rootworm, *Diabrotica barberi* Smith and Lawrence, have adapted to crop rotation, at least in certain parts of the Corn Belt. The western corn rootworm adapted by laying eggs in fields adjacent to corn (Levine and Oloumi-Sadeghi 1996), and the northern corn rootworm adapted by selecting for individuals that had an extended diapause and overwintered 1 or more additional year (Krysan et al. 1984, 1986). In areas where continuous corn is grown, insecticide is the most common management tactic (Mayo 1986). Resistance developed to larval treatment with cyclodiene insecticides >40 yr ago (Ball and Weekman 1962) and more recently to adult treatment with organophosphate and carbamate insecticides (Meinke et al. 1998). There are currently no practical alternatives to insecticides in continuous corn (Levine and Oloumi-Sadeghi 1991). These problems, possible implications of the Food Quality Protection Act of 1996 (Public Law 104-170), and expansion of their range into Europe (Sivcev et al. 1994) make additional strategies to manage corn rootworms highly desirable.

Host–plant resistance (both native and transgenic) may become a viable alternative to insecticides in the near future. Native resistance in corn has been reported that suffers significantly less damage than previous resistance sources (Hibbard et al. 1999a), and additional sources of native resistance have been identified and improved more recently (B.E.H., unpublished data). Transgenic corn that expresses endotoxins from the bacterium *Bacillus thuringiensis* Berliner (Bt) has been developed by several seed companies

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(Moellenbeck et al. 2001, Ellis et al. 2002) to control damage from western and northern corn rootworm larvae.

Because of the behavioral and genetic plasticity of these insects, adaptation to sources of native and transgenic resistance is a concern. If registered, transgenic sources of resistance are likely to reach the grower before native sources of resistance because of the difficulties of moving multigenic native traits into elite yielding germplasm. As part of the registration process for Bt crops in the United States, all registrants must submit an Insect Resistance Management Plan to the Environmental Protection Agency (EPA). Unfortunately, a number of gaps exist in our knowledge of corn rootworm biology that hinder the development of an optimal resistance management plan for these species. For example, we do not know whether rootworm larvae move between host plants after initial establishment. Movement of larvae from susceptible to transgenic plants and vice versa could adversely affect resistance management in several ways (Mallet and Porter 1992, Davis and Onstad 2000). Because larger larvae are more tolerant to toxins, initial development on a susceptible plant (a grassy weed or corn plant) followed by subsequent migration to a nearby transgenic plant could accelerate the rate of adaptation if heterozygotes with the resistance gene survived exposure to the toxin at greater rates. Alternatively, if a larva briefly fed on a transgenic root and then migrated to a nearby susceptible root, this too could accelerate the rate of resistance development if heterozygotes for the resistance gene were preferentially selected. However, if a low-dose product produced susceptible beetles, movement of larger larvae onto transgenic roots from less suitable alternate hosts or highly damaged corn in a seed mix could actually increase product durability by producing additional susceptible insects from within the transgenic field.

Information on the potential dispersal of larvae of the western corn rootworm is limited. According to the literature, western corn rootworm larvae can move up to 100 cm from egg hatch to where adults emerged (Suttle et al. 1967, Short and Luedtke 1970), although procedural problems make these data questionable (Branson 1986). Movement through the soil is affected by soil bulk density (Strnad and Bergman 1987a, Ellsbury et al. 1994), soil moisture (MacDonald and Ellis 1990), and macropores in the soil (Gustin and Schumacher 1989). Plant damage and lodging decreased when an artificial infestation point was 22.5 cm or farther from the plant when compared with infestation points 15 or 7.5 cm (Chaddha 1990). Other factors may also influence larval movement; for instance, western corn rootworm larvae are strongly attracted by carbon dioxide (Strnad et al. 1986, Hibbard and Bjostad 1988), which is released from respiring roots (Massimino et al. 1980). Factors in host roots trigger a localized search behavior when larvae are removed from the host and this localized search behavior is not triggered by nonhost roots (Strnad and Dunn 1990). Larval migration is not complete when the neonate reaches the plant. Strnad and Bergman (1987b) demonstrated that as larvae grow, they redistribute, moving to younger root whorls that emerge from the stalk. The extent of larval movement that occurs from plant to plant or from row to row within a cornfield after initial establishment is unknown and is likely to be affected by a number of factors including the proximity of roots from neighboring plants, the amount of competition for the current food source, and possibly soil structure and the quantity of favorable food sources in neighboring plants. Host location is done by neonate larvae, which are the most susceptible to transgenic and other toxins, but it is movement by larger larvae after initial feeding that is most important in rootworm resistance management because larger larvae are more tolerant to toxins. The primary objective of this study was to determine if post-establishment movement between plants and/or rows can occur.

Materials and Methods

The study was conducted in 1998 and 1999 at the University of Missouri Agronomy Research Center, 9.6 km east of Columbia, MO, which has a Mexico silt loam soil type. Soil composition at the site was determined to be 2% sand, 70% silt, and 28% clay (MU Soils Testing Laboratory). Each year the field selected for research had been planted with soybeans in the previous year, and unlike parts of the eastern Corn Belt, egg-laying by western corn rootworm adults outside of corn has not been detected in Missouri. Because of these two factors, we assumed that feral western corn rootworms would not be found in our plots, but we verified this with uninfested control.

1998 Experiments. Western corn rootworm larval movement over time was evaluated in four separate experiments differing in their combination of plant spacing (0.15 or 0.22 m) and row spacing (0.46 or 0.91 m). The experimental design was a completely random split-plot in space as outlined in Steel et al. (1997), with four replications and three sampling dates. The experimental design did not allow for statistical comparisons between blocks with different plant spacings and row spacings (comparisons between experiments cannot be made). The main plot was sample date and the subplot effect was plant category. All plots were planted with field corn (Pioneer Brand 3394) on 11 May. Immediately after an initial planting of both plant-spacing blocks (accomplished by changing gears on the planter), one-half of each plant-spacing block was cultivated to loosen the soil where tire tracks had driven. In this section, an additional row was hand-planted mid way between the two mechanically planted rows using the desired plant-spacing. Without cultivation, the soil was too compacted for normal hand planting.

Just after the majority of plants had germinated and emerged from the soil surface, i.e., at VE–V1 stage of growth (Ritchie et al. 1992), a central plant was artificially infested with 1,500 viable eggs (Fig. 1). Infestation was accomplished by hoeing a shallow depression (6–7 cm deep and 6 cm from the base) on each

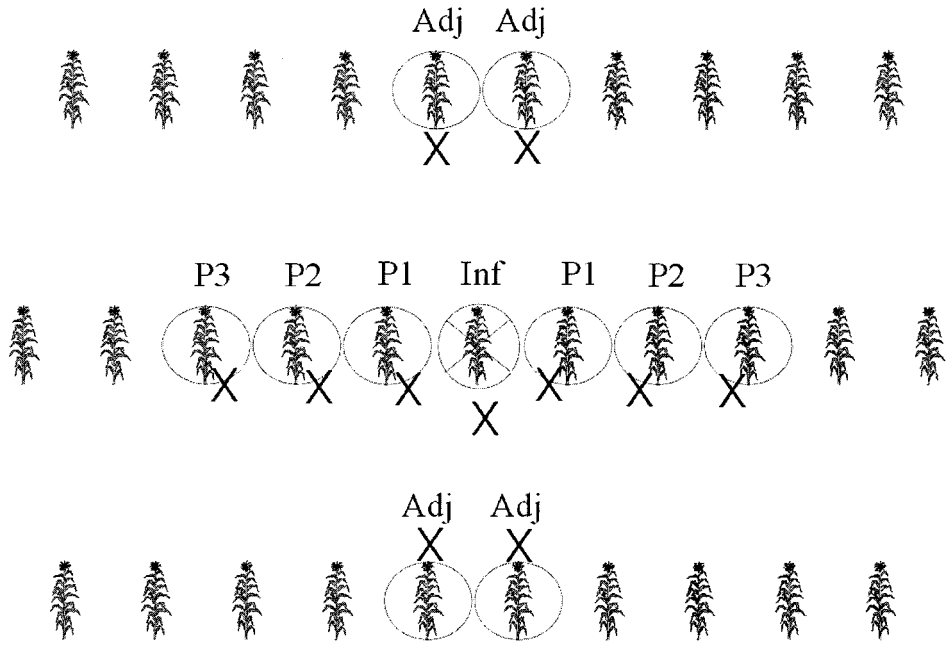

Fig. 1. Field plot design. The center plant was infested with 1,500 viable western corn rootworm eggs (one-half on each side), and soil core samples were taken at the approximate location of each X. Plots were established with all combinations of two row spacings (0.91 and 0.46 m) and two plant spacings (0.15 and 0.22 m).

side of the plant between rows and injecting 50 ml of a 0.15% agar solution in which 750 viable eggs (1,000 total eggs) had been suspended (Palmer et al. 1977). Fifteen hundred eggs is presumed to be greater than the number to which most plants are typically exposed in the Midwest, but this highly competitive situation was designed to optimize the chance of host changing after initial establishment, not how often this actually occurs under variable infestation levels in a continuous cornfield. Rootworm eggs were supplied from a laboratory-reared diapausing colony at the U.S. Department of Agriculture-Agriculture Research Service (USDA-ARS) Northern Grain Insects Laboratory in Brookings, SD. Damage from insects from this colony was not significantly different than damage caused by a similar number of feral insects in a previous study (Hibbard et al. 1999b). Plants chosen for infestation were located in portions of the field with 100% germination and were at least 1.5 m from any other infested plant. The infested plant was flagged, and the eggs were covered with soil.

Each infested plant formed the center of an 11-plant plot, which consisted of the infested plant, the three closest plants in the row on each side of the infested plant, and the two closest plants in each of the adjacent two rows (Fig. 1). Each plant fell into one of five categories: infested, p1, p2, p3, or adjacent row. Plots chosen for the two experiments in the 0.46-m row-spacing had no tractor or planter tire tracks in or between any of the three rows, and plots chosen for the two experiments in the 0.91-m row-spacing always had a tire track between the infested row and one (but not both) of the adjacent rows, so this row-spacing had two types of adjacent rows. For each of the four experiments, the center plant of at least 20 plots were infested so that each experiment could be sampled up to five different times with four replications each throughout the period western corn rootworm larvae were found in the field. On each sampling date, 4 of the 20 original plots were randomly chosen from those still available. In addition, four uninfested control plants were also sampled on each sample date to determine if feral populations of any corn rootworm species existed in the plots. Control plants were taken randomly from each of the four experiments and were at least 2 m away from any infested plant.

Larvae were sampled using a Turfmaster hole cutter (Turfmaster, Cedar Rapids, IA) to collect soil cores (10.2 cm diameter × 15.2 cm). Cores from the infested plant were taken adjacent to the stem on the row side of the plant and cores for the remaining 10 plants in each plot were taken from the side of the plant closest to the point of infestation, again at the base of the plant being sampled (Fig. 1). Each soil core was placed in a labeled plastic bag. The contents of the bags were then transferred to modified Berlése funnels, which used 40-watt bulbs as the heat source, and the cores were broken into smaller pieces. Edwards and Fletcher (1971) discussed a number of techniques for extracting soil arthropods. They noted that time to extraction can vary from 1 to 12 d, depending on the size of the sample and power of the heat source. Preliminary experiments under our conditions had shown that ≈95% of the larval recovery from the

Berlése funnels occurred within the first 72 h. In these early samples, a total of 90 larvae were recovered within 72 h, and a total of 5 additional larvae were recovered over the following week. For these experiments, samples were placed in the apparatus for a minimum of 72 h, after which time the jars were removed and larvae were counted and stored in 70% ethanol pending further analysis. A total of 180 Berlése funnels would have been required to process samples from all four experiments at the same time. Only 92 Berlése funnels were available, so only two of the four experiments (both plant-spacings within a row-spacing) were sampled on the same date, and the other one-half was usually sampled 3–4 d later.

Populations of the southern corn rootworm, *D. undecimpunctata howardi* Barber, rarely cause economic damage in Missouri, but adults of this species occasionally overwinter in Central Missouri and often migrate from the south in the spring. In 1998, 50 randomly selected ethanol-preserved larvae were closely examined for urogomphi, which are present on southern corn rootworms and not on western corn rootworms or northern corn rootworms (Krysan and Miller 1986). Distinguishing southern corn rootworm larvae is possible only for second and third instars. A number of verified southern corn rootworms (purchased from French Agricultural Research, Lamberton, MN) were reared in greenhouse pots for comparison to the field samples. No southern corn rootworms were found in the any of the field samples in 1998.

1999 Experiments. The four experiments set up in 1998 were repeated using the same experimental design, with changes and additions discussed below. All plots were planted entirely with a mechanical planter. For the blocks that were planted in 0.46-m rows, the 0.91-m planter was first offset by 0.23 m and driven in two passes in opposite directions with the tractor tires in the same location in both directions on 10 May. Again, plots chosen for the two experiments with a 0.46-m row-spacing had no tractor or planter tire tracks in or between any of the three rows, and plots chosen for the two experiments with a 0.91-m row-spacing always had a tire track between the infested row and one (but not both) of the adjacent rows.

Two additional sets of data were collected that were not collected in 1998. The western corn rootworm larvae recovered from the plots were weighed using an electronic balance (A&D model ER-182A; Apple Scientific, Chesterfield, OH) accurate to 0.00001 g, and the root masses from the infested plant and the four closest plants (two on each side within the row) were rated for rootworm feeding damage. Total larval weight (wet) and number were recorded from each Berlése sample. Insects that had been stored in 70% ethanol for a minimum of 48 h after collection from the Berlése funnels were gently rolled on dry filter paper to remove excess liquid, and all insects from one soil core were immediately weighed together. Dry weight was not taken because this would have destroyed morphological and DNA characteristics that distinguish western corn rootworm larvae from southern corn rootworm larvae. In addition, root damage ratings were collected from the infested plant and the four closest plants in a row. These roots were washed and rated for rootworm feeding damage using the node-injury scale (Oleson 1998) (http://www.ent.iastate.edu/pest/rootworm/nodeinjury/nodeinjury.html). This scale is based on the number of total nodes pruned. A rating of 3.0 is equivalent to three nodes of roots pruned to within 3.8 cm of the stalk, and equivalent to a 6 on the Hills and Peters (1971) scale. A rating of less than 1 indicates the decimal fraction of a node of roots damaged. Plants that were sampled for damage had already been sampled with soil cores, but this only damaged a small portion of the roots, and mechanical damage can be easily distinguished from roots pruned by insect feeding. In addition, three petri dishes containing several thousand eggs in moist soil were buried 6–7 cm deep at different locations throughout the field, but well away from any infested plant used in the experiment so that egg hatch initiation and duration could be more accurately determined. Just before and during the egg hatch period, the dishes were dug up every couple of days, the surface of each egg dish was visually examined for neonate larvae, and the dishes were replaced.

Much of Missouri had an unusually high southern corn rootworm infestation early in the season in 1999 (Bailey et al. 1999). Therefore, each larva that was collected was closely examined under a microscope for the presence of urogomphi. All of the southern corn rootworms were found in the early sample dates and were either late second or third instars. This compared with the neonates, first-, and a few early-second-instar western corn rootworms found during the same sampling dates. Most of the southern corn rootworm larvae had apparently pupated by 21 June. All southern corn rootworm larvae were excluded from further analysis. Extended diapause individuals of the northern corn rootworm was not known from Central Missouri, and fields in the area were scouted for northern corn rootworm, but none were found. All remaining corn rootworm larvae were assumed to be western corn rootworm larvae.

Soil Physics. Soil samples (5 cm diameter, 5 cm depth) were taken between rows and between plants in both 1998 and 1999 for the purpose of determining soil bulk density and air-filled porosity. Using field water content, parameters were estimated gravimetrically for each core sample (Brady 1990). Soil cores were taken on 18 June 1998 and 16 June 1999. In 1998, two core samples were taken from each combination of row and plant-spacing at three positions: within the row, between rows with a wheel track, and between rows without wheel tracks ($n = 24$). In 1999, three similar soil cores were taken for each plant-spacing in the 0.91-m rows at positions within the row, between rows with wheel tracks, and between rows without wheel tracks ($n = 18$), and for each plant-spacing in 0.46-m rows at positions within rows and between rows without wheel tracks ($n = 6$). These data were used to evaluate whether soil compaction may have played a role in larval movement between rows.

Statistical Analysis. The statistical package SAS (SAS Institute 1990) was used for data analysis. Data from each of the four experiments were analyzed

Table 1. ANOVA table for 1998

Experiment (Row/plant spacing [m])	Test	df	*F* value	*P* > *F*
1 (0.91/0.22)	Date	2, 36	7.09	0.0025
1 (0.91/0.22)	Plant	4, 36	14.39	0.0001
1 (0.91/0.22)	Date × plant	8, 36	13.15	0.0001
2 (0.46/0.22)	Date	2, 36	5.96	0.0058
2 (0.46/0.22)	Plant	4, 36	4.84	0.0031
2 (0.46/0.22)	Date × plant	8, 36	2.75	0.0177
3 (0.91/0.15)	Date	2, 36	3.43	0.0434
3 (0.91/0.15)	Plant	4, 36	5.57	0.0014
3 (0.91/0.15)	Date × plant	8, 36	2.26	0.0451
4 (0.46/0.15)	Date	2, 36	15.41	0.0001
4 (0.46/0.15)	Plant	4, 36	5.09	0.0024
4 (0.46/0.15)	Date × plant	8, 36	4.02	0.0017

separately in 1998 and 1999. The experimental design did not allow for statistical comparisons between blocks with different plant spacings and row spacings (comparisons between experiments cannot be made). All data were analyzed as a completely randomized split-plot in space as outlined in Steel et al. (1997). The linear statistical model contained the main plot effect of sample date, the subplot effect of plant category, and the interaction of sample date × plant category. Replicate within date served as the denominator of *F* for testing date. The residual error was used to test the subplot effects. Because no significant differences were found between the number of larvae recovered across a 0.91-m row that had tractor and planter tire traffic and the number of larvae recovered across 0.91-m row that did not have tire traffic, these data sets were combined in the final analysis of both experiments with 0.91-m row spacing in both years.

When analyzing for the number of larvae recovered, the treatments for each of the four experiments were arranged in a 3 × 5 (sampling date × plant category) split-plot in 1998 or a 4 × 5 split-plot in 1999 using PROC GLM. In 1999, average weight and plant damage were also analyzed. For each experiment, average weight was analyzed as a 3 × 5 split-plot (the last date was excluded), and plant damage was analyzed as a 4 × 3 split-plot (damage data were only collected for three plant categories). All data were transformed by $\log(x + 1)$ to meet the assumptions of equal variance in the analysis. Beyond the standard analysis of variance (ANOVA), we preplanned a comparison of plant categories across sampling dates, and this was done with an least significant difference (LSD) for a split-plot design as described by Steel et al. (1997). Data for plant categories with more than one plant per plot (see Fig. 1) were averaged on a per plant basis before the analysis. Control plants (the four plants on each sampling date randomly chosen from all four experiments) were not included in the analysis of any individual experiment because only one set of plants were collected for all four experiments.

Results and Discussion

Larvae Recovered per Plant. No western or northern corn rootworm larvae were recovered from any control plant in 1998 or 1999. In 1998, main affects of sampling date, plant category, and their interaction were significant for all four experiments (Table 1). The number of larvae recovered from the infested plant significantly decreased over time in each of the four experiments (Table 2). The number of larvae recovered from p1 plants significantly increased between the first and second sample dates in experiments 1 and 3 (note sample dates—these experiments were sampled first). The number of larvae recovered from p2 plants significantly increased between the first and second sample dates in experiment 1. No significant across row movement after initial establishment was found in 1998, even in the narrow 0.46-m row-spacings (Table 2). Across row movement that oc-

Table 2. Mean number of larvae recovered per plant in 1998 ± SE

Experiment (row/plant spacing [m])	Date	Infested	Plant category			Across row	Combined
			p1	p2	p3		
1 (0.91/0.22)	16 June	9.75 ± 2.63aA	0.25 ± 0.25bB	0.00 ± 0.00bB	0.00 ± 0.00aB	0.38 ± 0.24aB	2.08 ± 1.00a
1 (0.91/0.22)	25 June	1.00 ± 0.58bB	2.88 ± 0.55aA	1.50 ± 1.02aB	0.38 ± 0.38aB	0.38 ± 0.22aB	1.23 ± 0.32a
1 (0.91/0.22)	3 July	0.25 ± 0.25bAB	1.00 ± 0.46bA	0.25 ± 0.14bAB	0.13 ± 0.13aB	0.13 ± 0.13aB	0.38 ± 0.13b
1 (0.91/0.22)	Combined	3.67 ± 1.54A	1.38 ± 0.40B	0.58 ± 0.37C	0.17 ± 0.13C	0.29 ± 0.11C	
2 (0.46/0.22)	19 June	3.50 ± 1.19aA	0.88 ± 0.59aBC	1.75 ± 1.75aB	0.00 ± 0.00aC	0.19 ± 0.12aBC	1.26 ± 0.49a
2 (0.46/0.22)	29 June	1.25 ± 0.25bA	0.13 ± 0.13aB	0.13 ± 0.13aB	0.38 ± 0.13aAB	0.25 ± 0.14aB	0.43 ± 0.12ab
2 (0.46/0.22)	9 July	0.00 ± 0.00cA	0.25 ± 0.25aA	0.13 ± 0.13aA	0.13 ± 0.13aA	0.13 ± 0.07aA	0.13 ± 0.06b
2 (0.46/0.22)	Combined	1.58 ± 0.57A	0.42 ± 0.22B	0.67 ± 0.58B	0.17 ± 0.07B	0.19 ± 0.06B	
3 (0.91/0.15)	16 June	6.25 ± 3.94aA	0.25 ± 0.25bB	0.25 ± 0.14aB	0.00 ± 0.00aB	0.06 ± 0.06aB	1.46 ± 0.93ab
3 (0.91/0.15)	25 June	2.25 ± 0.63aA	3.38 ± 1.57aA	0.75 ± 0.25aAB	1.00 ± 0.68aAB	0.25 ± 0.18aB	1.53 ± 0.42a
3 (0.91/0.15)	3 July	0.50 ± 0.50bA	1.00 ± 0.41abA	0.50 ± 0.50aA	0.63 ± 0.31aA	0.00 ± 0.00aA	0.53 ± 0.17b
3 (0.91/0.15)	Combined	3.17 ± 1.45A	1.54 ± 0.64AB	0.50 ± 0.18BC	0.54 ± 0.26BC	0.10 ± 0.07C	
4 (0.46/0.15)	19 June	3.50 ± 1.50aA	3.25 ± 1.05aA	0.13 ± 0.13abB	0.38 ± 0.38aB	0.31 ± 0.24aB	1.51 ± 0.48a
4 (0.46/0.15)	29 June	0.50 ± 0.50bA	0.75 ± 0.32bA	0.75 ± 0.14aA	0.25 ± 0.14aA	0.44 ± 0.36aA	0.54 ± 0.14b
4 (0.46/0.15)	9 July	0.00 ± 0.00bA	0.13 ± 0.13bA	0.00 ± 0.00bA	0.00 ± 0.00aA	0.00 ± 0.00aA	0.03 ± 0.02c
4 (0.46/0.15)	Combined	1.33 ± 0.67A	1.38 ± 0.53A	0.29 ± 0.11B	0.21 ± 0.13B	0.25 ± 0.14B	

Different lowercase letters indicate a significant difference between dates within a plant category and within an experiment. Different uppercase letters indicate a significant difference between plant categories within a sample date and within an experiment. Although untransformed data and SE are shown, the statistical analysis was performed on $\log(x + 1)$ transformed data. Main effects from the ANOVA for differences between plant categories are in rows labeled "Combined" and main effects for sample date are in the column labeled "Combined"

Table 3. ANOVA table for 1999

Experiment (row/plant spacing [m])	Trait	test	df	*F* value	$P > F$
1 (0.91/0.22)	Larval no.	Date	3, 48	9.88	0.0001
1 (0.91/0.22)	Larval no.	Plant	4, 48	14.39	0.0007
1 (0.91/0.22)	Larval no.	Date × plant	12, 48	1.93	0.0534
2 (0.46/0.22)	Larval no.	Date	3, 48	16.65	0.0001
2 (0.46/0.22)	Larval no.	Plant	4, 48	4.76	0.0026
2 (0.46/0.22)	Larval no.	Date × plant	12, 48	1.80	0.0746
3 (0.91/0.15)	Larval no.	Date	3, 48	13.61	0.0001
3 (0.91/0.15)	Larval no.	Plant	4, 48	7.79	0.0001
3 (0.91/0.15)	Larval no.	Date × plant	12, 48	1.62	0.2973
4 (0.46/0.15)	Larval no.	Date	3, 48	10.69	0.0001
4 (0.46/0.15)	Larval no.	Plant	4, 48	5.99	0.0005
4 (0.46/0.15)	Larval no.	Date × plant	12, 48	2.41	0.0158
1 (0.91/0.22)	Avg. wt.	Date	2, 15	21.58	0.0001
1 (0.91/0.22)	Avg. wt.	Plant	4, 15	1.51	0.2479
1 (0.91/0.22)	Avg. wt.	Date × plant	7, 15	0.38	0.9022
2 (0.46/0.22)	Avg. wt.	Date	2, 18	21.46	0.0001
2 (0.46/0.22)	Avg. wt.	Plant	4, 18	1.10	0.3874
2 (0.46/0.22)	Avg. wt.	Date × plant	6, 18	0.91	0.5094
3 (0.91/0.15)	Avg. wt.	Date	2, 13	13.46	0.0007
3 (0.91/0.15)	Avg. wt.	Plant	4, 13	0.62	0.6577
3 (0.91/0.15)	Avg. wt.	Date × plant	8, 13	0.85	0.5757
4 (0.46/0.15)	Avg. wt.	Date	2, 10	24.57	0.0001
4 (0.46/0.15)	Avg. wt.	Plant	4, 10	1.60	0.2478
4 (0.46/0.15)	Avg. wt.	Date × plant	7, 10	1.13	0.4183
1 (0.91/0.22)	Damage	Date	3, 24	30.40	0.0001
1 (0.91/0.22)	Damage	Plant	2, 24	36.18	0.0001
1 (0.91/0.22)	Damage	Date × plant	6, 24	7.52	0.0001
2 (0.46/0.22)	Damage	Date	3, 24	10.88	0.0001
2 (0.46/0.22)	Damage	Plant	2, 24	11.21	0.0004
2 (0.46/0.22)	Damage	Date × plant	6, 24	2.63	0.0421
3 (0.91/0.15)	Damage	Date	3, 24	9.87	0.0002
3 (0.91/0.15)	Damage	Plant	2, 24	22.71	0.0001
3 (0.91/0.15)	Damage	Date × plant	6, 24	2.29	0.0688
4 (0.46/0.15)	Damage	Date	3, 24	11.59	0.0001
4 (0.46/0.15)	Damage	Plant	2, 24	15.91	0.0001
4 (0.46/0.15)	Damage	Date × plant	6, 24	2.41	0.0575

curred in 1998 primarily occurred in initial host location by neonate larvae. Apparently, not all of the larvae went to the closest roots available on egg hatch.

Overall, in the combined data for each experiment, the mean number of larvae recovered per plant decreased over the sampling dates, and very few larvae were recovered on the final sampling date (Table 2). By 3 July and 9 July, we observed pupae in our samples. Pupae were generally not recovered using the Berlése technique, at least partially accounting for lower recovery on the last sampling date for each experiment.

The lower number of larvae recovered from the infested plants over time in all four experiments, the higher number of larvae recovered from the p1 over time in experiments 1 and 3, and the higher number of larvae recovered from p2 plants over time in experiment 1 (Table 2) initially suggested that larvae moved from the infested plant after establishment. However, we did not document the onset and duration of egg hatch nor the weight of recovered larvae in 1998. Larvae found on the p1 plant the second sampling date could have been newly hatched larvae that went directly to the p1 plant after hatch. Because of these problems, egg hatch initiation, duration, larval weight gain, and plant damage were recorded in 1999.

In 1999, main effects of sampling date and plant category were significant for the number of larvae recovered in all four experiments, but their interaction was only significant for experiment 4 (Table 3). As indicated by egg dishes placed in the field at infestation depth, egg eclosion began sometime between 10 June and 14 June and ended sometime between 18 June and 22 June. In experiment 1, the number of larvae recovered from p3 plants significantly increased over time, and in experiment 2, the number of larvae recovered from the adjacent row plants and the p2 plants significantly increased over time (Table 4). In experiment 2, plants in the adjacent row were actually closer to the infested plant than those plants within the row three plants away. The number of larvae recovered from the infested plant initially increased for all but experiment 4 but then significantly decreased for each of the four experiments (Table 4). Larvae moved up to three plants down the row (experiment 1) and across a 0.46-m row (experiment 2) after initially establishing on the infested plant. The number of larvae recovered from adjacent row plants in experiments 1 and 3 did not significant increase over time, indicating that larvae did not cross a 0.91-m row. Statistically significant movement after initial establishment was not documented for either experiment 3 or 4, perhaps because we initiated sampling from these experiment after some movement had already taken place. An average of one or more larvae was recovered from the

Table 4. Mean number of larvae recovered per plant in 1999 ± SE

Experiment (row/plant spacing [m])	Date	Infested	Plant category			Across row	Combined
			p1	p2	p3		
1 (0.91/0.22)	12 June	0.75 ± 0.75bcB	1.75 ± 0.25aA	0.50 ± 0.20abAB	0.00 ± 0.00bB	0.25 ± 0.18aB	0.65 ± 0.20b
1 (0.91/0.22)	22 June	3.75 ± 1.31aA	2.25 ± 1.18aA	1.38 ± 0.59aAB	0.38 ± 0.24bBC	0.13 ± 0.13aC	1.58 ± 0.45a
1 (0.91/0.22)	28 June	1.25 ± 0.75bAB	2.38 ± 0.90aA	1.88 ± 0.72aA	2.50 ± 1.21aA	0.13 ± 0.13aB	1.63 ± 0.38a
1 (0.91/0.22)	6 July	0.00 ± 0.00cA	0.25 ± 0.14bA	0.13 ± 0.13bA	0.13 ± 0.13bA	0.00 ± 0.00aA	0.10 ± 0.05c
1 (0.91/0.22)	Combined	1.44 ± 0.52AB	1.66 ± 0.40A	0.97 ± 0.30AB	0.75 ± 0.38BC	0.13 ± 0.06C	
2 (0.46/0.22)	12 June	0.50 ± 0.29bcAB	1.25 ± 0.60bA	0.00 ± 0.00bB	0.25 ± 0.14aAB	0.00 ± 0.00bB	0.40 ± 0.16b
2 (0.46/0.22)	22 June	4.25 ± 1.65aA	4.38 ± 2.06aA	1.63 ± 0.31aAB	0.25 ± 0.14aC	0.56 ± 0.26abBC	2.21 ± 0.63a
2 (0.46/0.22)	28 June	1.25 ± 0.63bA	1.25 ± 0.14bA	1.75 ± 0.85aA	0.50 ± 0.35aA	0.81 ± 0.21aA	1.11 ± 0.23a
2 (0.46/0.22)	6 July	0.00 ± 0.00cB	0.00 ± 0.00cA	0.13 ± 0.13bA	0.00 ± 0.00aA	0.06 ± 0.06abA	0.04 ± 0.03b
2 (0.46/0.22)	Combined	1.50 ± 0.58A	1.72 ± 0.64A	0.88 ± 0.29AB	0.25 ± 0.10B	0.36 ± 0.12B	
3 (0.91/0.15)	18 June	2.50 ± 1.55aA	2.38 ± 0.90aA	1.25 ± 0.83abAB	0.50 ± 0.50aB	0.06 ± 0.06aB	1.34 ± 0.43a
3 (0.91/0.15)	25 June	3.25 ± 0.63aA	2.38 ± 1.09aAB	2.25 ± 0.63aA	0.63 ± 0.13aBC	0.13 ± 0.13aC	1.73 ± 0.37a
3 (0.91/0.15)	1 July	0.25 ± 0.25bA	1.00 ± 0.35abA	0.63 ± 0.38bcA	0.13 ± 0.13aA	0.19 ± 0.19aA	0.44 ± 0.13b
3 (0.91/0.15)	9 July	0.25 ± 0.25bA	0.13 ± 0.13bA	0.00 ± 0.00cA	0.00 ± 0.00aA	0.00 ± 0.00aA	0.08 ± 0.05b
3 (0.91/0.15)	Combined	1.56 ± 0.52A	1.47 ± 0.41A	1.03 ± 0.33A	0.31 ± 0.14B	0.09 ± 0.06B	
4 (0.46/0.15)	18 June	4.50 ± 2.18aA	1.75 ± 0.92aB	1.00 ± 0.46aB	0.00 ± 0.00aC	0.06 ± 0.06aC	1.46 ± 0.57a
4 (0.46/0.15)	25 June	0.75 ± 0.48bAB	1.00 ± 0.20aA	0.63 ± 0.47abAB	0.13 ± 0.13aB	0.56 ± 0.19aAB	0.61 ± 0.15ab
4 (0.46/0.15)	1 July	0.50 ± 0.50bA	0.63 ± 0.31abA	0.38 ± 0.13abA	0.13 ± 0.13aA	0.25 ± 0.18aA	0.38 ± 0.12b
4 (0.46/0.15)	9 July	0.00 ± 0.00bA	0.00 ± 0.00bA	0.00 ± 0.00bA	0.00 ± 0.00aA	0.00 ± 0.00aA	0.00 ± 0.00c
4 (0.46/0.15)	Combined	1.44 ± 0.69A	0.85 ± 0.28A	0.50 ± 0.18AB	0.06 ± 0.04C	0.22 ± 0.08BC	

Different lowercase letters indicate a significant difference between dates within a plant category and within an experiment. Different uppercase letters indicate a significant difference between plant categories within a sample date and within an experiment. Although untransformed data and SE are shown, the statistical analysis was performed on $\log(x + 1)$ transformed data. Main effects from the ANOVA for differences between plant categories are in rows labeled "Combined" and main effects for sample date are in the column labeled "Combined."

p2 plants on their first sampling date (Table 4). Sampling for these two experiments was initiated 6 d after sampling was initiated on the first two experiments. Although we cannot prove where the larvae initially established, by 18 June, a higher proportion of larvae were recovered from p2 and p3 plants than were recovered from these plants on 12 June in experiments 1 and 2 (Table 4). Overall, few larvae were recovered from the fourth sampling date in 1999. It is likely that many of the larvae had pupated by this time (some pupae were seen when breaking up soil cores for the Berlése funnels), and pupae are not recovered with the behavioral technique used in this experiment.

Larval Weight. As expected from larval growth and a tight hatching interval, the main affect of sampling date was significant for average weight in all four experiments (Table 3). The main affect of plant category was not significant for average weight for any of the experiments, nor was their interaction (Table 3). The lower degrees of freedom for average weight was because larvae were not recovered on every plant. In these cases there was a total weight of zero, but no average weight. Also, on the 6 July and 9 July 1999 sample dates, very few larvae were recovered from any of the treatment combinations, so the final sampling date was excluded from the average larval weight analysis as described above.

In the combined analysis, average larval mass significantly increased over the sampling dates for each of the four experiments (Table 5). These results document that larvae recovered on later sampling dates did not recently eclose in that location, even from plants farther from the infested plant. Interestingly, by the third sampling date, the average weight of larvae recovered from p3 plants was significantly greater than the average weight of larvae recovered from the infested plant in three of the four experiments (Table 5). We do not know from our data whether larger larvae tended to move more or larvae that moved grew faster. However, because the roots of the infested plant tended to be highly damaged by the third sampling date, larvae that moved did find a less damaged food source.

Root Damage. The main effects of sampling date and plant category were significant for root damage in all four experiments (Table 3). The interaction of these two main effects was significant in experiments 1 and 2 and nearly significant in experiments 3 and 4. Root damage ratings increased significantly over time in all four experiments on the infested plant, the p1 plant, and the combined analysis (Table 6). Damage levels were highest on the infested plant and significantly decreased on more distal plants (Table 6). Damage averaged 2.25 nodes of roots pruned to within 3.8 cm of the stalk the infested plant on the last sampling date for experiment 4 (Table 6).

Soil Physics. Soil samples from 1998 had an average bulk density of 1.48 ± 0.02 mg/m^3 between rows where tractor and planter tracks had been, 1.45 ± 0.03 mg/m^3 between rows without tire tracks, and 1.43 ± 0.03 mg/m^3 within rows. Percentage pore space was 44.04 ± 0.90, 45.92 ± 1.30, and 45.14 ± 0.96, respectively, from the same locations. Soil samples from 1999 had an average bulk density of 1.49 ± 0.01 mg/m^3 between rows where tractor and planter tracks had been, 1.30 ± 0.03 mg/m^3 between rows without tire tracks, and 1.26 ± 0.02 mg/m^3 within rows. Percent pore space was 43.62 ± 0.34, 50.93 ± 1.11, and 52.31 ± 0.77, respectively, from the same locations. Strnad and Bergman (1987a) found that larvae did not move >5

Table 5. Average wet weight (mg) of larvae recovered per plant in 1999 ± SE

Experiment (row/plant spacing [m])	Date	Infested	Plant category			Row	Combined
			p1	p2	p3		
1 (0.91/0.22)	12 June	0.33 ± n/a aA	1.25 ± 0.39bA	1.69 ± 0.63bA	n/a ± n/a	1.17 ± 0.29aA	1.27 ± 0.27b
1 (0.91/0.22)	22 June	0.77 ± 0.18aA	1.35 ± 0.39bA	1.28 ± 0.54ba	2.73 ± 1.18bA	2.63 ± n/a aA	1.49 ± 0.31b
1 (0.91/0.22)	28 June	3.04 ± 0.49aB	6.57 ± 2.93aAB	5.96 ± 0.64aAB	8.87 ± 2.84aA	2.99 ± n/a aAB	6.33 ± 1.20a
1 (0.91/0.22)	Combined	1.45 ± 0.55B	3.05 ± 1.17B	2.81 ± 0.77B	6.82 ± 2.26A	1.99 ± 0.51B	
2 (0.46/0.22)	12 June	1.65 ± 1.10aA	0.49 ± 0.27bA	n/a ± n/a	2.13 ± 0.69bA	n/a ± n/a	1.29 ± 0.51b
2 (0.46/0.22)	22 June	2.25 ± 0.45aA	1.58 ± 0.26bA	2.22 ± 0.61bA	1.15 ± 0.42bA	1.68 ± 0.72aA	1.87 ± 0.25b
2 (0.46/0.22)	28 June	4.96 ± 1.24aB	5.48 ± 1.36aB	9.70 ± 3.85aAB	13.13 ± 1.96aA	5.75 ± 1.83aB	7.20 ± 1.18a
2 (0.46/0.22)	Combined	3.02 ± 0.72A	2.81 ± 0.90A	5.42 ± 2.28A	5.47 ± 2.55A	4.00 ± 1.31A	
3 (0.91/0.15)	18 June	0.57 ± 0.13aA	0.55 ± 0.18aA	0.86 ± 0.31bA	2.80 ± n/a aA	0.93 ± n/a aA	0.85 ± 0.22c
3 (0.91/0.15)	25 June	2.24 ± 1.06aA	2.39 ± 1.26aA	3.58 ± 1.07abA	2.06 ± 1.08aA	3.35 ± n/a aA	2.61 ± 0.49b
3 (0.91/0.15)	1 July	3.10 ± n/a aB	5.15 ± 0.79aAB	6.02 ± 0.44aAB	8.95 ± n/a aA	1.87 ± n/a aB	5.17 ± 0.81a
3 (0.91/0.15)	Combined	1.72 ± 0.61A	2.47 ± 0.74A	3.51 ± 0.81A	3.33 ± 1.32A	2.05 ± 0.71A	
4 (0.46/0.15)	18 June	0.68 ± 0.38aA	0.64 ± 0.26bA	0.44 ± 0.15bA	n/a ± n/a	0.60 ± n/a aA	0.60 ± 0.15b
4 (0.46/0.15)	25 June	1.48 ± 0.69aA	3.41 ± 0.78aA	4.20 ± 1.84aA	2.00 ± n/a aA	4.19 ± 0.65aA	3.30 ± 0.54a
4 (0.46/0.15)	1 July	1.70 ± n/a aA	3.08 ± 1.05aA	5.53 ± 0.64aA	1.65 ± n/a aA	4.53 ± 2.62aA	3.83 ± 0.82a
4 (0.46/0.15)	Combined	1.05 ± 0.34B	2.48 ± 0.59AB	3.29 ± 1.02A	1.83 ± 0.18AB	3.71 ± 1.19A	

Different lowercase letters indicate a significant difference between dates within a plant category and within an experiment. Different uppercase letters indicate a significant difference between plant categories within a sample date and within an experiment. Although untransformed data and SE are shown, the statistical analysis was performed on $\log(x + 1)$ transformed data. Main effects from the ANOVA for differences between plant categories are in rows labeled "Combined" and main effects for sample date are in the column labeled "Combined."

cm in silt loam soil with a density of 1.3 mg/m^3. Five of six of our samples averaged above this level for both years. Gustin and Schumacher's (1989) data supported Strnad and Bergman (1987a) conclusions in artificial environments without structured pores, but they found that if a structured pore were added to the equation (such as an earthworm hole, decaying root in field situations), larval movement was not hampered. Ellsbury et al. (1994) demonstrated that survival and establishment of western corn rootworm larvae were associated with greater soil pore continuity in uncompacted plots.

On a per-plant basis, more western corn rootworm larvae were recovered from the infested plant than from all the other plant categories put together in three of the four experiments in 1998, whereas in 1999, the sum of larvae recovered from the other plant categories was nearly twice the number recovered from the infested plant (Table 4). Bulk density was lower and percent pore space was higher in 1999 than in 1998 except for traffic areas, perhaps contributing to the greater overall larval movement in 1999. Other factors such as food availability likely also played a role. One possible reason for more larvae moving away

Table 6. Root damage per plant in 1999 ± SE using the node-injury 0 to 3 damage scale

Experiment (row/plant spacing [m])	Date	Infested	Plant		Combined
			p1	p2	
1 (0.91/0.22)	12 June	0.16 ± 0.05cA	0.18 ± 0.06bA	0.16 ± 0.05bA	0.17 ± 0.03c
1 (0.91/0.22)	22 June	1.50 ± 0.54aA	0.78 ± 0.50aB	0.78 ± 0.45aB	1.02 ± 0.28a
1 (0.91/0.22)	28 June	0.94 ± 0.30bA	0.A64 ± 0.17aA	0.34 ± 0.15bB	0.64 ± 0.13b
1 (0.91/0.22)	6 July	1.79 ± 0.36aA	0.77 ± 0.19aB	0.19 ± 0.07bC	0.92 ± 0.24a
1 (0.91/0.22)	Combined	1.10 ± 0.23A	0.59 ± 0.14B	0.37 ± 0.12C	
2 (0.46/0.22)	12 June	0.07 ± 0.02cA	0.18 ± 0.16bA	0.10 ± 0.05aA	0.11 ± 0.03c
2 (0.46/0.22)	22 June	0.75 ± 0.42bA	0.40 ± 0.17abA	0.32 ± 0.11aA	0.49 ± 0.15ab
2 (0.46/0.22)	28 June	0.63 ± 0.13bA	0.39 ± 0.17abAB	0.17 ± 0.04aB	0.40 ± 0.09b
2 (0.46/0.22)	6 July	1.26 ± 0.22aA	0.64 ± 0.12aB	0.21 ± 0.08aC	0.71 ± 0.15a
2 (0.46/0.22)	Combined	0.68 ± 0.15A	0.40 ± 0.07B	0.20 ± 0.04C	
3 (0.91/0.15)	18 June	0.59 ± 0.19cA	0.47 ± 0.27bA	0.49 ± 0.19abA	0.52 ± 0.12b
3 (0.91/0.15)	25 June	1.00 ± 0.20bA	0.50 ± 0.15abB	0.29 ± 0.07bB	0.60 ± 0.12b
3 (0.91/0.15)	1 July	0.98 ± 0.35bcA	0.70 ± 0.31abA	0.29 ± 0.10bB	0.65 ± 0.17b
3 (0.91/0.15)	9 July	1.85 ± 0.34aA	0.86 ± 0.28aB	0.66 ± 0.20aB	1.12 ± 0.21a
3 (0.91/0.15)	Combined	1.10 ± 0.17A	0.63 ± 0.12B	0.43 ± 0.08B	
4 (0.46/0.15)	18 June	0.51 ± 0.33cA	0.30 ± 0.09bA	0.28 ± 0.09aA	0.36 ± 0.11b
4 (0.46/0.15)	25 June	0.56 ± 0.24cA	0.37 ± 0.14bA	0.23 ± 0.09aA	0.39 ± 0.10b
4 (0.46/0.15)	1 July	1.75 ± 0.34bA	1.09 ± 0.42aA	0.36 ± 0.07aB	1.07 ± 0.24a
4 (0.46/0.15)	9 July	2.25 ± 0.32aA	1.19 ± 0.43aB	0.34 ± 0.06aC	1.26 ± 0.29a
4 (0.46/0.15)	Combined	1.27 ± 0.24A	0.74 ± 0.17B	0.30 ± 0.04C	

Different lowercase letters indicate a significant difference between dates within a plant category and within an experiment. Different uppercase letters indicate a significant difference between plant categories within a sample date and within an experiment. Although untransformed data and standard error are shown, the statistical analysis was performed on $\log(x + 1)$ transformed data. Main effects from the ANOVA for differences between plant categories are in rows labeled "Combined" and main effects for sample date are in the column labeled "Combined."

from the infested plant in 1999 than in 1998, could be the high level of larval injury to the infested plant. Southern corn rootworm larvae contributed to this damage, and southern corn rootworm damage likely peaked when larvae were first becoming established. Noticeable root damage (0.1–0.5 on the node-injury scale) occurred even before the western corn rootworm eggs hatched (B.E.H., unpublished data). The reason for the apparent disappearance of southern corn rootworm larvae later in the season remains unknown. Although the number of larvae significantly increased over time on roots as far down the row as the p3 plant (Table 4), damage did not significantly increase over time on the p2 plant (Table 6). Nearly all damage between 14 June and 22 June was probably caused by the southern corn rootworm. During this early interval, western corn rootworm eggs were hatching or at the neonate stage and could not have caused an appreciable amount of damage.

In conclusion, post-establishment movement by western corn rootworm larvae was clearly documented in two of four treatment combinations in 1999 where larvae moved up to three plants down the row and across a 0.46-m row. Larvae did not significantly cross a 0.91-m row in 1998 or 1999, whether or not the soil had been compacted by a tractor and planter. In 1998, it initially appeared that post-establishment movement had been documented at least one plant down the row, but those insects that were found on p1 on the second sampling date could have moved directly to the p1 plant after hatching. This explanation could also apply for p2 plants in 1998, but is less likely.

Inferences drawn from this study must be taken within context. First, our data were collected in only one soil type. Second, although larval movement after establishment was clearly documented, this was so in only two of eight experiments in 2 yr, and the experiments were done in an artificial situation. In a typical field situation with susceptible corn, eggs will not be present near one plant that is surrounded by plants without eggs. Our data do not provide significant insight into how larvae might disperse when all plants in an area are heavily damaged or when only moderate damage occurs. However, if transgenic roots are not repellent, our data, which were generated with undamaged plants surrounding highly damaged plants, may be especially applicable. A transgenic plant in a seed mixture with highly damaged plants nearby may attract larvae because of the mass of roots available. The same may occur in block or strip plantings of narrow-row corn. If these larvae develop initially on susceptible plants, they would likely be larger and more tolerant of the transgenic toxin, perhaps hastening the development of resistance if heterozygotes with the resistance gene survived exposure to the toxin at greater rates. However, if a low-dose product such as Monsanto's Cry3Bb produced susceptible beetles (not documented at this point), movement of larger larvae onto a transgenic roots from less suitable alternate hosts or highly damaged corn in a seed mix could actually increase product durability by producing additional susceptible insects from within the Bt field.

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